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Exposure to Bright Light Has Little Effect on Eye Sensitivity and Ultrastructure of *Saduria entomon* (Crustacea; Isopoda; Valvifera)

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ABSTRACT—Specimens of the isopod *Saduria entomon* were caught during late winter nights in Finland and divided into three groups: one was not at all exposed to any light and served as the control; a second was exposed to midday sunlight of 9.1×10^{20} qu/m^{2}s for 30 min; the third was exposed to artificial white light of 4.2×10^{20} qu/m^{2}s during the day for 30 min. The visual sensitivity thresholds as well as V/log I curves of 15 exposed animals from 30 min to 456 h postexposure were recorded at random intervals and compared with values obtained from nine control animals. Only a very minor reduction of sensitivity in exposed animals was noticed. Parallel ultrastructural studies confirmed that light-induced structural derangements of visual membranes, known to occur in other species, were minimal, with an enlargement of microvilli to twice their normal diameter being the most obvious. Spectral sensitivity curves recorded from nine control animals reverased one single peak to light of 550 nm wavelength, close to maximum transmission of the water in which the animals occur. The results show that apparently not all crustaceans possess eyes that are easily damaged by bright light and—in view of the light-induced sensitivity loss reported in *Mysis relicta* (13)—highlight the danger of attempting to predict how photoreceptors of another species would respond, even if the species occurred in the same habitat.

INTRODUCTION

In several species of crustaceans it was noticed that exposure to even moderate levels of brightness could suppress visual sensitivity for several days, if not longer [1, 2, 3, 4]. Anatomical studies in parallel with the physiological observations have revealed the light-induced photoreceptor damage or breakdown, once triggered, continued to proceed in the dark long after the initial exposure to light [4–9], and, at least in *Jasus edwardsii* [4] and *Boreomysis megalops* [10], had a direct impact on the behaviour.

Crustaceans that normally inhabit environments of low ambient light levels [2, 7, 9], or are primarily noctural [4, 8] seem to be especially at risk. A further aggravating factor appears to be higher than usual temperature [11, 12]. Having earlier published, in this journal, a thorough analysis of light-induced sensitivity loss and subsequent recovery in the opossum shrimp *Mysis relicta* [13], we decided to follow up that study with an investigation into the effects of bright light on the visual properticas and ultrastructure of the eye of *Saduria entomon*, an isopod species that frequently shares the same habitat with *Mysis relicta*. The results from this investigation clearly show that even in species inhabiting seemingly identical environments, a reliable prediction on how the photoreceptors would respond to an exposure of bright light in other species in difficult, if not impossible.

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MATERIALS AND METHODS

Electrophysiology

Experimental animals of various size and sexes were collected in traps at 5–20 m depth from the

Eastern Baltic Sea off Tvärminne Zoological Station and brought to the surface during winter nights in complete absence of artificial lights. All handling was done with the aid of "Find-R-Scope" infra-red viewers. Captured animals were maintained in the laboratory for several weeks at 5–6°C under totally dark conditions and served as controls. Some of the animals were exposed to the midday sun at an intensity of 9.1×10^{20} qu/m^{2}s for 30 min from 12.50 to 13.20 hr in water of 6°C. A wide beaker placed in a white plastic trough served as the holding receptacle during exposure. The outside temperature happened to be the same as the water temperature. Animals treated in this way are referred to as "sunexposed animals".

Animals exposed to artificial, white light, 4.2×10^{20} qu/m^{2}s in intensity, are referred to as "light-exposed". The set-up during the 30 min exposure to artificial light consisted of a 1000 ml glass beaker (diameter 100 mm) filled with 600 ml of water. The beaker was insulated from stray light with a styrox collar at the height of the water level. Light spectrum and intensity were measured with a QSM 2500 quantum spectrometer under identical conditions through the bottom of the beaker (without animals). This means the there was an extra glass bottom between sensor and the light source. The light source consisted of two Argaphoto-BM-200 V/500W photolamps 50 cm over the bottom of the beaker. The lamps were cooled by two electric fans and the temperature of the water surrounding the animals was thermostatically controlled and reached a maximum of 8°C.

Following the exposures to either artificial or sun light, the animals were immediately returned to their dark environments, but kept separate from non-exposed control animals. Tests of post-exposure visual sensitivity commenced as early as 30 min and continued for up to 456 hr thereafter. Forty-one animals altogether were examined electrophysiologically, but only about 2/3 lasted throughout the experiment and could be evaluated.

Experimental procedures closely followed those reported previously [2, 13]. During preparation, using infra-red image converters mounted on a Wild-5 stereomicroscope, each animal was illuminated by light that had passed through 2 Kodak Wratten 87 gelatin filters and sometimes a heat filter as well, which were inserted in the ray path of white light coming from a microscope lamp. The incident light, perpendicular to the eye surface, was centered around the hole through which the recording electrode was lowered 40–50 μm into the eye. The light spot made by the stimulating flash was large enough to cover the entire eye. Always the same region of the eye was aimed for when inserting the electrode. Following preparations, which, on average, did not take longer than 10 min, the test animals were given 30 min in total darkness to recuperate from the operation. The system for stimulation consisted of an extended source (Osram 6B, 15W microscope lamp, powered by a constant voltage device) and all recordings were made in the AC-setting. Fourteen narrow band spectral interference filters, covering wavelengths from 406 to 673 nm, were available to test spectral sensitivity. Flash duration was 0.5 sec.

At the completion of the recording the eye and position of the electrode were examined under the microscope; head and body of the experimental animals were then preserved in alcohol.

Electron microscopy

For ultrastructural observations by transmission electron microscopy a number of eyes from animals representing controls as well as those that had been exposed to sun or artificial lights for 30 min and then allowed to recuperate in the dark for 30 min, 24 hr, and 41 hr, were carefully removed from the heads and cut free from surrounding tissue in a procedure that did not take longer than 2 min. The eyes were prefixed for 12 hr in sodium-cacodylate-buffered 2 1/2% glutaraldehyde, transferred to buffer, and postfixed three weeks later for 2 hr in sodium-cacodylate-buffered 2% OsO_4. Dehydration was achieved in the usual way and followed by embedding in Epon. Sections for electron microscopy were cut with a Reichert OMU2 ultramicrotome, stained in uranylacetate and lead citrate for a few min each, and examined under a Philips 400 TEM.

RESULTS

Electrophysiology

ERG-waveforms of two main shapes were recorded, although by far the most common one was a rapid initial cornea-negative "on-response" followed by a slightly slower return to the baseline. This kind of response was virtually identical to that of the eye of the isopod *Cirolana borealis* [2]. Another type of response that seemed to come from eyes in which the electrode and made less optimal contact, i.e. either did not penetrate the corneal hole well or had been pushed into the eye too far, displayed a posititve overshoot immediately following the initial negative deflection. Where responses of this type were used for the analysis, as with all other responses too, only the amplitude of the initial negative deflection was considered. This made comparisons between animals consistent. All eyes responded to increasing light intensities with an increase in amplitude. The highest peak amplitude recorded was 3050 μV in a fully dark-adapted animal, but in the majority of eyes tested peak amplitudes were in the vicinity of 1000 μV.

Spectral sensitivity, measured from the eyes of seven control specimens, peaks at 550 nm and then falls off towards both shorter and longer wavelengths. There was little variation in the seven specimens studied, hence the small standard deviations at all wavelengths tested (Fig. 1). Maximum sensitivity is situated close to the region of maximum transmittance of the water in this area (approx. 565 nm [3]), which suggests that the animals may be considered well-adapted to the local photic environment.

Taking a response of 50 μV as threshold level, we compared absolute sensitivities to white light in animals of different lengths and different degrees of dark-adaptation (Fig. 2). No statistically significant correlation with size (and, therefore, presumably age) of the animal was found ($R=0.045$). Animals that had been exposed to artificial light

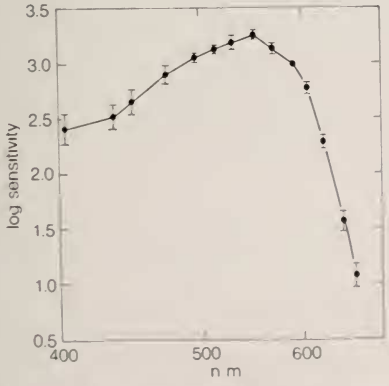


Fig. 1. Spectral sensitivity curve of *Saduria entomon*, based on recordings from seven different animals. Standard deviation for each wavelength tested is indicated by vertical bars. The single maximum (550 nm) is situated in the region of maximum light transmission of the water column (approx. 565 nm). Abscissa: the wave-length plotted upon a linear scale of frequency.

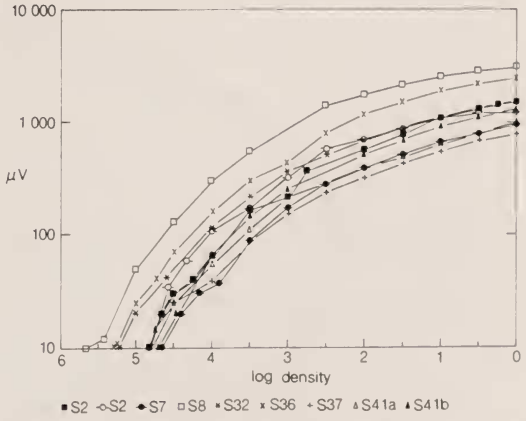


Fig. 2. A comparison of the eye's sensitivity with the animal's size (monitored as telson length) reveals on correlation.

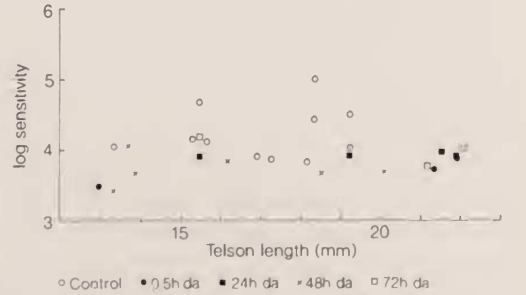


Fig. 3. V/log I (=response/stimulus intensity) data of nine control animals not exposed to light prior to the recordings, plotted on log-log axes. Threshold sensitivities cluster around a log I of -5 and amplitudes around 1000 μV. Different symbols represent different animals.

before, did, however, display a trend of reduced sensitivity, which prompted further examination.

V/log I curves of nine control animals are shown in Figure 3. Taking most and least sensitive curves, they are distributed across a sensitivity band roughly 1 log unit wide and display some variation in maximum amplitude, but basically they are very similar in shape. V/log I curves of seven animals tested from 3 hr to 456 hr of dark-adaptation following a 30 min exposure to sunlight, form a cluster with little variation between one another (Fig. 4). Likewise, the V/log I curves of all thirteen animals exposed for 30 min to artificial light, fall within the limits set by the five curves shown in Figure 5, representing the extreme dark-adaptation times 0.5 hr and approx. 70 hr. A further 4 V/log I curves, representing light-exposed animals tested between 22 and 28 hr post-exposure and another 4 from 41–48 hr post-exposure animals have been recorded (not shown) and fall exactly within the cluster of curve shown in Figures 4 and 5.

In the study of the mysid compound eye [13], it was found that a useful indication of the degree of light-induced sensitivity reduction was provided by an examination of the 50-100 μV response span

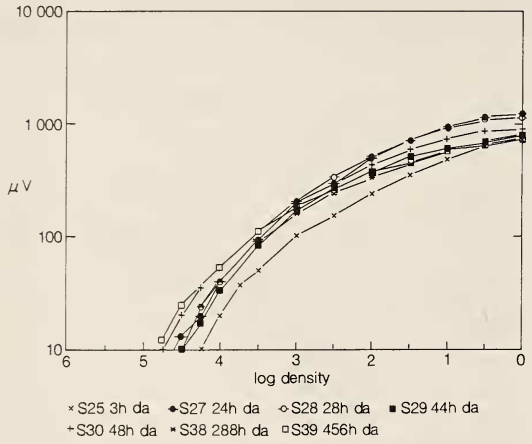


Fig. 4. V/log I data of seven animals obtained at indicated times of dark adaptation (da) following a 30 min exposure to midday sunlight of 9.1×10^{20} qu/m^{2}s intensity. Irrespective of whether testing was carried out three hours postexposure (animal S25) or 456 hr postexposure (animal S39), the difference between these and the control curves of Fig. 3 is very small.

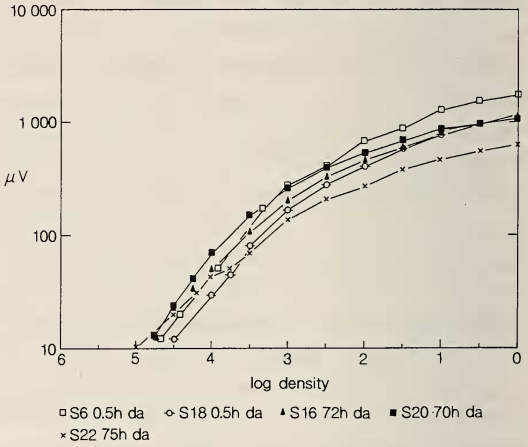


Fig. 5. V/log I data of five animals obtained at indicated times of dark-adaptation (da) following a 30 min exposure to artificial light of 4.2×10^{20} qu/m^{2}s during the day. Irrespective of whether testing was carried out 0.5 hr (animal S6) or 75 hr (animal S22) postexposure, the difference between these, the curves generated by sun-exposed animals, and the controls is very minor.

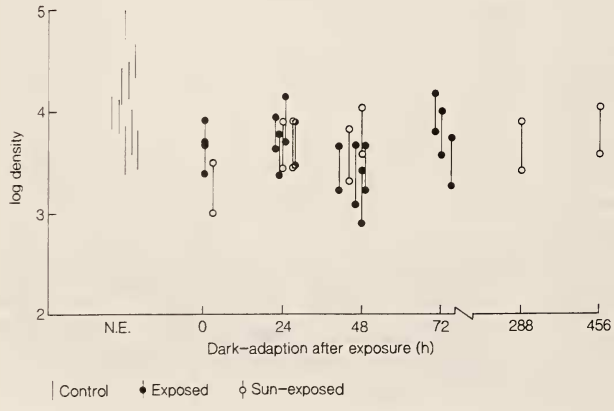


Fig. 6. Responses of 50 μV and 100 μV and their corresponding stimulus intensities (on the ordinate) in relation to postexposure time plotted on the abscissa. Note the slightly elevated sensitivities of the non-exposed control group but the rather uniform span of the 50–100 μV bar on all animals tested.

and its associated neutral density range (Fig. 6). For each group the mean log density value causing a 50 μV response was calculated. Both exposure groups differed on a statistically significant level from the control group (t-test, control versus light-exposed, $t=3.21$; $p=0.008$ and control versus sun-exposed $t=2.75$; $p=0.018$). No significant differences showed up between sun and artificial light exposed animals. In contrast to the *Mysis* data [13], the length of the 50–100 μV bar is virtually identical in controls, sun- and light-exposed animals and only the position of the bar in relation to associated neutral densities varies slightly between the groups. This suggests that all animals, irrespective of their previous exposure history, apparently possess well-functioning eyes, albeit with slightly different thresholds.

Another parameter looked at was the difference between the neutral densities responsible for giving rise to 50 μV and 100 μV responses (Fig. 7). As in the mysid study [13], this parameter describes the slope of the V/log I curves. Thus, the significantly high value of this parameter for the sun-exposed group as compared with the control group ($t=-5.31$; $p=0.0003$) and the light-exposed group ($t=-2.25$; $p=0.04$) demonstrates a shallower slope for the V/log I curve of the sun-exposed group. No statistically significant difference between control and artificial light group was revealed.

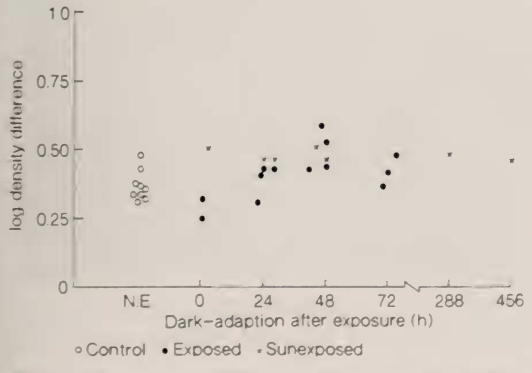


FIG. 7. Log-density difference between stimuli giving rise to 50μV and 100 μV responses plotted against control-, sun-, and artificial light exposed animals, tested at postexposure times indicated on the abscissa.

Histology

Dissection of the eye, because of the very hard cuticle surrounding it, proved difficult, but adequately fixed material from eyes of 11 animals was analyzed by electron microscopy. An overview of gross ommatidiae organisation is shown in Figure 19. There were few screening pigment granules surrounding the crystalline cones and, it agreement with Nilsson [18], no changes were found in light and in darkness. Transversely sectioned rhabdoms of animals, whether or not exposed to light, displayed a variety of sizes and shapes and were often 5-lobed with diameters between opposite lobes of around 30 μm (Figs. 8, 9, 11). Screening pigment granules were moderate in number and occupied peripheral positions in dark-adapted animals. The number of contributing retinula cells was normally five, although two smaller additional ones were usually present and sometimes were seen to have a small rhabdomere as well. Rhabdoms stained uniformly and even in eyes of animals exposed to sunlight and artificial lights the majoirty of the rhabdoms retained their integrity and staining characteristics known from the controls. Central regions of abnormal microvilli isolated from apparently undamaged and relatively unaltered rhabdom by an electron-translucent gap did develop in some eyes 24 hr postexposure to sunlight (Fig. 9).

Irregularities and a loosening of the microvillar compound occurred in some ommatidia of the light-exposed, 24 hr post-exposure eye (Fig. 10). However, in all eyes examined 24 hr and 41 hr post-exposure, screening pigment granules in the dark-adapted peripheral positions and the overall picture of retinula cells and rhabdoms was that of near-normality (Fig. 11). Since the mictovilli are the structures not only most at risk from photo-induced structural damage, but also represent the site of photo-transduction and are, thus, a good structural indicator of "function", a closer look at their organization seemed an essential requirement for this investigation.

In animals that had been in the dark for at least two weeks prior to fixation, microvilli exhibited an extremely regular lattice of parallel oriented, blind-ending tubes, measuring 65-75 nm in dia-

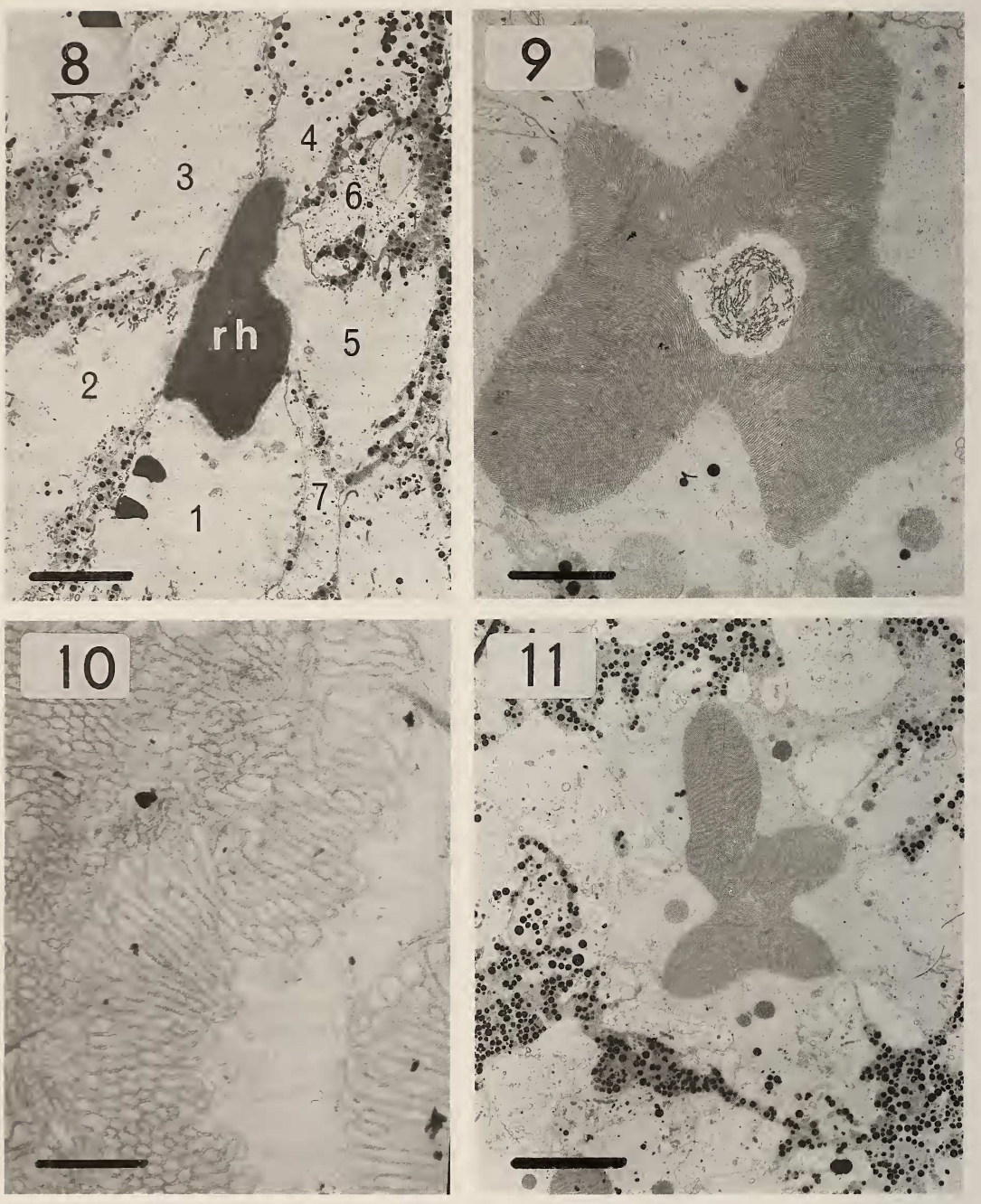


FIG. 8. *S. entomon* rhabdoms (Rh) come in various shapes, but typically measure approximately 30 μm across. They are made up of five major and two minor retinula cells (numbered 1–7). In this dark-adapted control animal screening pigment granules are located peripherally. The scale is 10 μm.

FIG. 9. Some rhabdoms like this of a 30 min sun-exposed animal fixed 24 hr postexposure in the dark, display central lesions. Most of the rhabdom and its constituent microvilli, however, are intact and screening pigment granules are generally in the dark-adapted position. The scale is 5 μm.

FIG. 10. A certain degree of loosening of the microvillar arrangement and serrations at the edges of the rhabdom were found in material exposed for 30 min to artificial light and then fixed 24 hr after recuperation in the dark.

meter (Figs. 12, 13). The regular and dense packing of the microvilli resulted in hexagonal profiles of the latter when sectioned transversely (Fig. 12). As with microvilli of other crustaceans, their cytoplasmic interior was in communication with the retinula cell plasma, althought bundles of microvilli seemed to arise from the same anchor point similar to the situations described from lobster [14] and crayfish [15].

A 30 min exposure to artificial light resulted in few signs of microvillar disruption 30 min post-exposure (Fig. 14). Rhabdom microvilli were still regular, though suggestions of swellings in amongst them were apparent. The edges of the rhabdom exhibited signs of light-adaptation in the form of vesicles budding off towards the retinula cell and screening pigment granules were in the light-adapted position (Fig. 15). Twenty-four hours post-exposure a considerable proportion of microvilli had become enlarged (Fig. 16), a feature also seen in the eye of *Mysis relicta* as a consequence of bright light exposure [13].

Although a greater variety of microvillar dimensions and orientations than in the dark-adapted control rhabdoms was obvious in eyes exposed to bright light, the overall impression was that of relatively undisturbed rhabdoms. The swelling of the microvillar diameters to at least twice the size of those of the dark-adapted controls was the most obvious change. Forty one hours post-exposure microvillar diameters had become reduced, but still had not reached the pre-exposure dark-adapted control dimensions (Fig. 17).

Animals exposed to the somewhat brighter sunlight for 30 min exhibited similar trends, but on a lesser scale. For example, signs of rhabdom damage, confined to the central portion of some rhabdoms, were indeed seen 24 hr post-exposure (Fig. 9). But microvillar diameters 30 min postexposure were virtually unchaneged from dark-adapted controls as well as 24 hr post-exposure eyes (Fig. 18).

DISCUSSION

In view of the many publications describing light-induced sensitivity loss and ultrastructural damage in crustacean photoreceptors, summarised in [13], the result that in *Saduria entomon* exposure to sun and artificial lights had very little effect, comes as a surprise. *S. entomon* can hardly be termed an animal that habitually or frequently gets exposed to sunlight. On the contrary; it spends most of its time in or near the bottom mud of the Baltic Sea and is clearly nocturnal throughout the year [24]. It is, however, extremely tolerant to changing salinities [16] and copes with a wide range of oxygen concentrations and temperatures as well [25]. At present we can not offer an exhaustive explanation as to why the eyes of some isopods like the deepwater species *Cirolana borealis* and *Bathynomyus giganteus* apparently lose all sensitivity [2, 9] and react with a disintegration of the rhabdom to an exposure of bright light [6, 9] while others including the Antarctic *Clyptonotus antarcticus* [17] and *Saduria entomon* (this paper) suffer little structural and/or functional effect.

Saduria has a fairly thick, multilayered cornea (approx. 30–40 μm; this paper) and so has *Glyptonotus* (approx. 70 μm [17]) but we do not believe that corneal thickness and ultrastructure alone are the reason for the greater light tolerance in these two species, for *Cirolana borealis* which reacts sensitively to bright light exposure [2, 6] also has rather thick corneal lenses (20–55 μm: [18]), and the same dichotomy is observed in the amphipods *Orchomene plebs* and *O.* sp. cf. *rossi* [7, 11]. The duration of the initial exposure to light was twice as long in *Mysis relicta* [13], but the intensity of the light used was much lower than that used in this study. This, too, points to a more fundamental difference in the eye physiology of the two species.

An interesting structural parallel to *M. relicta* [13] offer the enlarged microvillus diameters in the eye of *Saduria*, following exposure to bright light.

The scale is 15 μm.

FIG. 11. Approximately two days following 30 min of exposure to sunlight, rhabdoms of animals subsequently kept in the dark like this example are apparently normal and, apart from a small remnant of the central lesion seen earlier, quite indistinguishable from control animals. The scale is 10 μm.

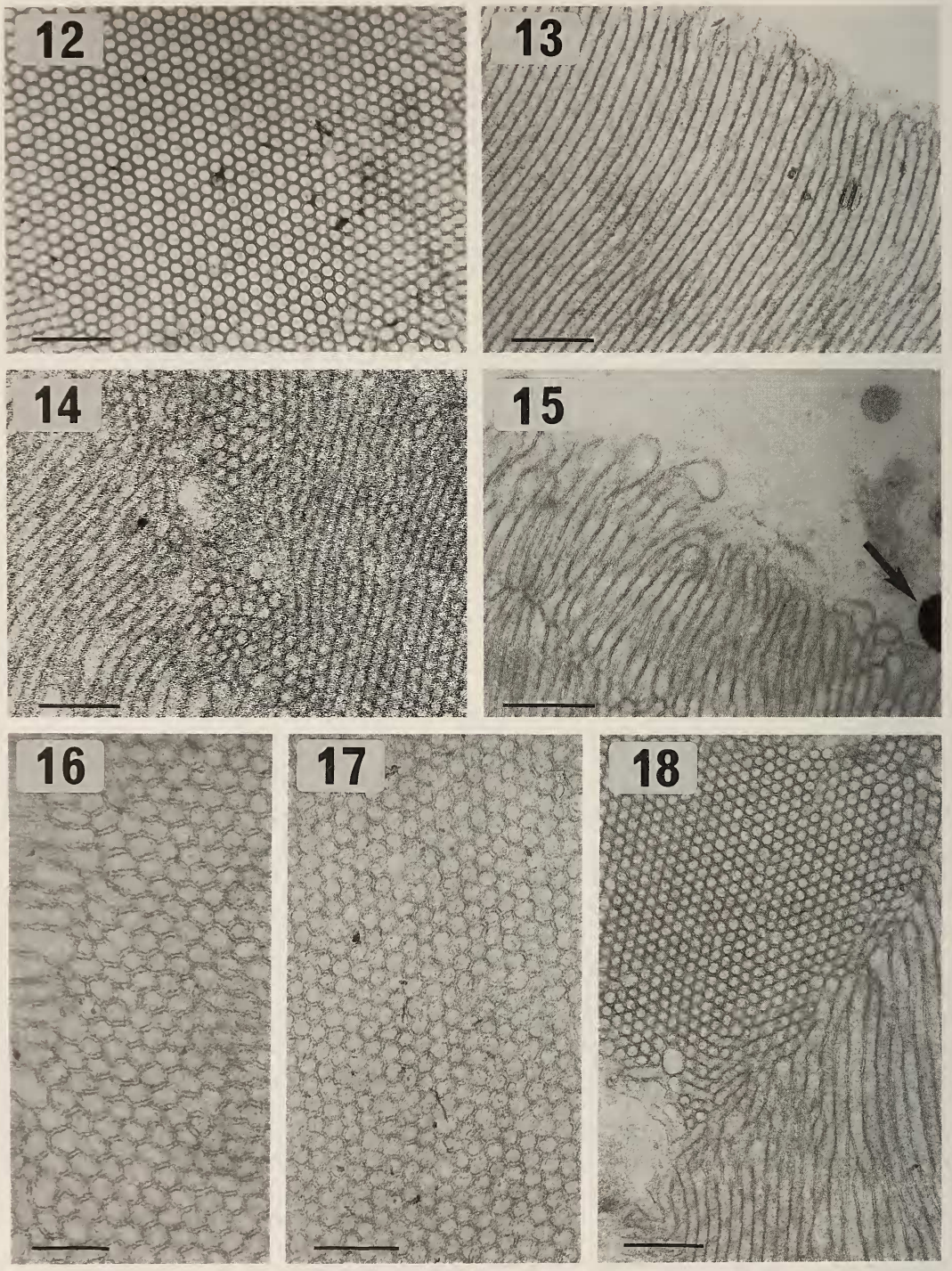
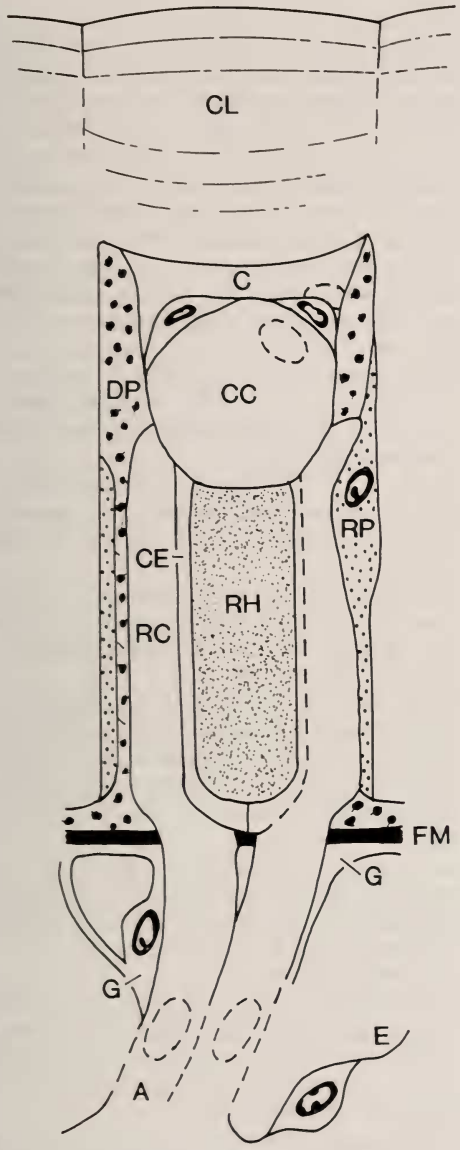


Fig. 12. Rhabdom microvilli of dark-adapted, control animals display a regular array of hexagonally-packed tubes measuring 65–75 nm in diatmeter. The scale is 0.5 μm.

Fig. 13. When longitudinally-sectioned, the microvilli of rhabdoms of dark-adapted control animals display a paralle alignment, a uniform diameter of 70 nm and anchor-points at the edge of the cytoplasm shared by a group of



But while in *M. relicta* the loosening of the microvillus compound led to a worsening state culminating in a severe derangement of microvilli, the *Saduria* eye possessed sufficient "self-healing" powers to go back to normal. The minor nature of the structural damage was completely mirrored by the ERGs, recorded pre- and post-exposure. While there was a statistically significant difference in the thresholds and the way the V/log I curves began to rise within the first 50 μV (between 50 and 100 μV amplitudes), the effect was very minor when compared with the dramatic sensitivity loss and flattening of V/log I curves in *M. relicta* under very similar experimental conditions [13]. In fact, the higher sensitivities in the dark-adapted controls showed an overall, greater scatter than those recorded post-exposure. This indicates to us that the unnaturally long period the controls have spent in total darkness might have increased the amounts of photo-pigment to abnormally high levels, which then raises the question, whether the small microvillus diameters observed in the dark-adapted controls can be considered normal—or abnormally small. In any case, there can be absolutely no doubt of the ability of the exposed eyes to function normally over a wide range, covering more than 4 log units, of photic stimulation even following the exposure to bright light.

FIG. 19. Schematic representation of longitudinal section of ommatidial unit in the eye of *Saduria entomon* (after Nilsson [18]). A = axon; CC = crystalline cone; CE = cone cell extension; CL = corneal layers; DP = distal pigment; E = eye capsule membrane; FM = fenestrated membrane; G = glial cell; RC = retinula cell; RH = rhabdom; RP = reflecting pigment.

microvilli. The scale is 0.5 μm.

FIG. 14. After thirty minutes in the dark following a 30 min exposure to artificial lights, microvillar diameters are still apparently unchanged from controls, but a certain degree of disruption of the regular order is becoming apparent. The scale is 0.5μm.

FIG. 15. Same treatment as in FIG. 14, but the focus is on the edge of the rhabdom where typical signs of light-exposure like budding vesicles, screening pigment grains (arrow), are apparent. The scale is 0.6 μm.

FIG. 16. In all three animals in which rhabdoms were examined one day follwing exposure to artificial light for 30 min, the microvillar organization for the greater part remained intact, but microvillar dimensions had changed with diameters now being 2–3 times as wide as the controls. The scale is 0.5 μm.

FIG. 17. Even 41 hr following exposure to artificial light, microvillus diameters are not back to the control values The scale is 0.5 μm.

FIG. 18. A touch of light-induced irregularities in the organization and dimensions of microvilli is also observed in 30 min sun-exposed rhabdoms. But at 24 hr postexposure (this micrograph), the rhabdom is barely different from the control. The scale is 0.5 μm.

The spectral sensitivity curve with its single maximum in the green part of the spectrum appears to reflect a high degree of evolutionary adaptation to the light transmission properties of Tvärminne offshore waters, which exhibit a maximum at around 565 nm [3]. Spectral sensitivity apparently does not undergo any change with size (and, therefore, presumably age) of the animals, which agrees with recent studies by Ziedins and Meyer-Rochow [19] on *Petrolisthes elongatus* and Forward and Cronin [20] on intertidal crabs. Seasonal changes, however, documented in the crayfish by Nosaki [21] and Suzuki *et al.* [22] as well as variations between geographically isolated populations, reported for example in *Mysis relicta* by Lindström and Nilsson [3] cannot be ruled out.

What this study has made abundanly clear is that generalizations are dangerous. Even crustacean species co-inhabiting the same environment may display very differnt responses to the exposure of bright light. In the words of Nilsson [23], who presented three examples of crustaceans with "apparently the 'wrong' type of eye", one is forced to accept "how easy it is to underestimate the competence of evolution".

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